TRACHYPACHIDAE AND HYDRADEPHAGA (COLEOPTERA): A MONOPHYLETIC UNIT?[1]

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Members of *Trachypachus* represent an extremely interesting phylogenetic relic taxon, probably derived from near the branching point of Caraboidea and Dytiscoidea (Bell, 1966; Evans, 1977). Most investigations of the phylogenetic position of *Trachypachus* have been done by morphologists and/or carabidologists. The purposes of this paper are to: 1. bring this taxn to the attention of hydradephagan workers and to call for their views, 2. summarize the contributions of these workers, 3. point out some of the problem areas in hydradephagan phylogeny, 4. test the presumption that Trachypachidae belongs with Hydradephaga, and 5. re-evaluate the monophyly of Hydradephaga itself.

My working hypothesis is that the suborder Adephaga comprises two monophyletic lineages: Caraboidea and Dytiscoidea, the latter including Trachypachidae and Hydradephaga. Trachypachids have traditionally been placed within Carabidae, at the tribal level, on the basis of possession of tibial antennal cleaner, carabiform adult and larval habitus and terrestrial life style. Trachypachidae contains two genera: *Trachypachus* and *Systolosomus,* together including six extant species. Trachypachidae were first recognized to be of importance to discussions of hydradephagan evolution by Crowson (1955) who elevated the tribe to family status. Specimens of *Systolosomus* are not common in collections and none were examined during this study. Sharp (1882) and Hammond (1979) described structural details of *Systolosomus* and concurred with other authors that these two genera are closely related. Hydradephaga presently includes Amphizoidae, Hygrobiidae, Haliplidae, Noteridae, Dytiscidae and Gyrinidae.

Cladistic methods were used. For an explanation of this technique see Hennig (1966) and Kavanaugh (1972, 1978) and the references cited therein. Polarity of characters was determined by comparison to character states found in presumed sister groups. Dytiscoidea and Caraboidea are almost certainly sister groups with Dytiscoidea being derived from an ancestor which probably would be placed within the division Isochaeta of Carabidae (Bell, 1966). For Dytiscoidea, characters are polarized from plesiotypic states exhibited by members of Caraboidea.

This analysis would be strengthened if character states for the primitive sister group of Adephaga could be determined. Unfortunately this taxon is

probably something other than an extant member of Coleoptera and perhaps is best represented by members of the extinct suborder Protocoleoptera (*sensu* Crowson, 1975), known only from fossils of Lower Permian age. Crowson (1975) listed the character states known for this group. The extant group nearest to the ancestor of Adephaga are probably Megaloptera (Crowson, 1975).

Discussion of Characters

The best treatment of imaginal structure of Hydradephaga remains Sharp's (1882, pp. 190–257) analysis of "Dytiscidae." Sharp's concept of Dytiscidae includes the currently accepted families Amphizoidae, Hygrobiidae, Noteridae and Dytiscidae *s. str.* Throughout his discussion Sharp compared dytiscids to carabids and haliplids in sufficient detail to provide good structural knowledge of most of Dytiscoidea. This account should be supplemented by Hatch's (1926) work on gyrinid structure. Sharp (1882, pp. 967–972) also analyzed similarities and differences in character states between Carabidae and Dytiscidae *sensu* Sharp, some of which were missed by later authors.

The following discussion is restricted to those characters in which the majority of Dytiscoidea exhibit the apotypic states. Distribution of character states among various groups of Adephaga is shown in Table 1.

Character 1. Antennal pubescence. Antennae of all adult hydradephagans are glabrous or almost glabrous. The apex of each antennomere of adult *Trachypachus* does have setae, but antennomeres I–X lack the close set pubescence common in adult Caraboidea (Bell, 1966; Hammond, 1979; Sharp, 1882). However, antennomere XI does have a small area of pubescence. A similar condition was found in adult members of some Pseudomorphini and Scaritini (Sharp, 1882) and in Gehrinigiini (Bell, 1966) of Carabidae. This is a weak synapomorphy because it is a loss state (Hecht and Edwards, 1976).

Character 2. Prosternal process. Characteristic of adults of Dytiscoidea is an elongate, well-developed prosternal process (Sharp, 1882), although it is somewhat less well-developed in gyrinids (Hatch, 1926). Members of Protocoleoptera and most Caraboidea do not have the prosternal process as well-developed as in Dytiscoidea (Crowson, 1975; Sharp, 1882). Possible reasons for increased importance of the prosternal process may be inferred from an ecological and structural perspective. Concomitant with an increase in body streamlining is a decrease in size of the prosternum (Nachtigall, 1974). This has resulted in a decrease in ventral contact of procoxae with the prosternum but is compensated for by an increase in dorsal contact to produce articulation around a wheel-like rim (Evans, 1977). The prosternal process forms a strong union between the prothorax and the remainder of

the sternum. The benefits of such a union are a major increase in structural integrity and protection of this major and potentially vulnerable body joint by thick cuticle (Hlavac, 1972). The latter would be very important to hydradephagan beetles which respire at the water surface and thereby expose their venters to attack by predators. A well-developed prosternal process is also found in adults of the carabid genera *Omophron* (Omophronini) and *Cyclosomus* (Masoreini) (Sharp, 1882).

Character 3. Open procoxal cavities with post-coxal bridge. All adult Dytiscoidea, in which this character has been investigated possess open procoxal cavities and a post-coxal bridge formed by extension of the prosternum and proepimeron (Bell, 1965, 1966, 1967; Baehr 1979). This condition is distinct from closed procoxal cavities in which a coxal bar is present (Bell, 1966, 1967). It is also found in adult members of *Carabus* (Carabini), *Hiletus* (Hiletini) and *Leistus* (Nebriini) of Carabidae (Hlavac, 1975).

Characters 2 and 3 could form a functional complex in that a change in the prosternal process could be correlated with a change in the type of procoxal cavity. If this can be demonstrated then Characters 2 and 3 should be treated as a single character.

Character 4. Prosternal-metasternal contact. Contact of the prosternal process with the metasternum is common to most Hydradephaga and there is no such contact in adult Protocoleoptera and most Caraboidea (Crowson, 1975; Sharp, 1882). Prosternal-metasternal contact is possible because the mesosternum is shortened and occupies an almost vertical rather than a horizontal plane. The cavity thus formed conceals the prothoracic legs of larger dytiscids during swimming—a hydrodynamic co-adaptation (Nachtigall, 1974). Smaller dytiscids use all three pairs of legs for locomotion (Nachtigall, 1974), and in some groups (*i.e.* some Bidessini and Vatellini of Hydroporinae) prosternal-metasternal contact appears to be secondarily lost. Adult *Trachypachus* also have shortened mesosterna, but they are not as vertical as in most Hydradephaga. Actual contact of the prosternal process with the metasternum can be attained only by maximum deflection of head and prothorax. The question is whether this is due to resumption of a more typically caraboid (*i.e.* terrestrial) life style or whether it represents a truly primitive step in the evolution of the character. Within Carabidae, only adult *Cyclosomus* (Masoreini) have prosternal-metasternal contact.

Adult member of Gyrinidae have the prosternum contacting the mesosternum (Sharp, 1882; Hatch, 1926). In gyrinids, the mesosternum is horizontal rather than vertical. Therefore, streamlining has taken a different form in response to life on the water surface habitats rather than the subsurface habitats of other Hydradephaga. Flexibility of the prosternal joint would be important to life on the water surface. As well, a near vertical mesosternum in gyrinids would represent an extreme, antistreamlined con-

dition (Nachtigall, 1974). Possession of the plesiotypic state by adult hali-plids remains unexplained.

Character 5. Metacoxal cavities of interrupted type. All adult dytiscoids have metacoxae which are extended laterally to reach the elytral epipleura, *i.e.* metacoxal cavities of the interrupted type (Bell, 1965, 1966, 1967). Members of Gehringiini and Rhysodini of Carabidae also possess this character state, although they are believed to have achieved it independently (Bell, 1967). Most adult Caraboidea and Protocoleoptera have uninterrupted coxal cavities (Bell, 1967; Crowson, 1975).

Character 6. Metacoxal fusion. In trachypachids and hydradephaga the metacoxae are fused medially, the fusion being marked by a single internal intercoxal septum continuous with the metafurca and the median sternal ridge (Evans, 1977). This metacoxal immobilization of Dytiscoidea is un-doubtedly related to their aquatic existence. The metasternum and meta-coxae function as a single sclerite and great expansion of the metacoxae is coincident with expansion of coxal swimming muscles (Evans, 1977). Ad-aptation to aquatic existence has allowed a change in function of metacoxae from femoral counter-rotation in the wedge-pushing movement of Caraboi-dea to the propulsion movement of Dytiscoidea (Evans, 1977). It is inter-esting to note that Evans (1977) believes that metacoxal immobilization has been achieved in a different manner among members of Haliplidae than by other members of Dytiscoidea.

Character 7. Setal patch of flight wings. Microtrichia of the metathoracic wings of some Dytiscoidea are organized into a distinct setal patch just posterior to vein Cu_2 near the wing margin (Ward, 1979). This setal patch acts as a mechanism for binding the flight wings against a roughened area on the underside of the elytra and together they function in wing-folding (Hammond, 1979). Among adult Adephaga the setal patch is found in tra-chypachids, amphizoids, most dytiscids and most noterids (Hammond, 1979; Ward, 1979). It has presumably been secondarily lost in certain genera among Bidessini, Hydrovatini and Hyphydrini (Hydroporinae: Dytiscidae), whose adults are quite small, and within some members of Notomicrini and Noterini of Noteridae (Hammond, 1979).

Character 8. Giardina body. Within the ovaries of some female dytiscoid beetles, development of oogonia is similar to that of most insects having polytrophic ovarioles up until the preoocyte stage of oogenesis. At this stage an extrachromosomal Giardina body appears. The accepted role for the Giardina body is that the extrachromosomal DNA which it contains is the nucleolus organizing region of the genome responsible for synthesis of ri-bosomal RNA (Urbani, 1969).

In insects, Giardina bodies are known only in females of *Acheta* (Gryl-lidae: Orthoptera), *Tipula* (Tipulidae: Diptera) and Dytiscoidea (Urbani

1969). The Giardina bodies appear to be of a different type in Dytiscoidea than in other insects. Too little study has been devoted to the distribution of this character within Dytiscoidea and closely related groups for its real value as a synapomorphy to be ascertained. It is known from representatives of Gyrinidae, Hygrobiidae, Colymbetinae and Laccophilinae (Dytiscidae). Among investigated Dytiscinae (Dytiscidae) it is absent in members of *Eretes* (Eretini) and *Cybister* (Cybistrini) but present in members of *Hydaticus* (Hydaticini), *Acilius* (Thermonectini) and *Dytiscus* (Dytiscini). It was not found in the single member of Hydroporinae studied (Urbani, 1969), and there is no information about Trachypachidae, Amphizoidae, Haliplidae and Noteridae.

Character 9. Size and armature of internal sac. The great majority of male caraboids have, within the median lobe of the aedeagus, a well-developed internal sac equipped with setae and spines known as armature (Jeannel, 1955). Male dytiscoids have the internal sac greatly reduced or absent and I have not seen any published reports of armature within the internal sac. The character states of members of Protocoleoptera is unknown, but I have interpreted the dytiscoid state as apomorphic. The problems of interpreting this character have to do with reduction and character polarity. Character states exhibited by dytiscoids could be: derived once and indicate monophyly; achieved independently through reduction from the caraboid state and give a false impression of monophyly; or, they could be the primitive form of the character with the caraboid type being derived, in which case, it would be invalid to use for monophyly.

Character 10. Dilator muscle of vagina. Adult female Dytiscoidea possess a muscle which originates on the upper surface of the vulvar sclerite and inserts dorsolaterally on the vagina, termed dilator of the vagina by Burmeister (1976). This muscle was absent from all caraboids examined by Burmeister and appears to have been secondarily lost from some members of Bidessini and Hydroporini (Hydroporinae: Dytiscidae).

Analysis of Distribution of Characters

Trachypachids possess nine of 10 synapomorphies with Hydradephaga, and the tenth has not been investigated within this group. Amphizoids, hygrobiids, noterids, gyrinids and the dytiscid subfamilies Laccophilinae, Colymbetinae and Dytiscinae each have a majority of apomorphic states.

One difficulty affecting deduction of relationships among Adephaga is the age of the groups. Division into Caraboidea and Dytiscoidea (Geadephaga and Hydradephaga) was probably complete by the end of the Triassic period and most extant families were present before the end of the Jurassic (Crowson, 1975). The great age of these two superfamilies greatly increases the chances of evolutionary change, specialization and modification which could

Table 1. Characters, character states and their distribution among family-level taxa of Adephaga. Only those used in phylogenetic analysis of the monophyly of Dytiscoidea are included. Character polarity is based on ex-group comparison to Protocoleoptera and Caraboidea.

Character no. and description	Character states		Dytiscoidea								Exceptions within a family-level taxon with a majority of one character state
				Hydradephaga							
	Plesiomorphic (−)	Apomorphic (+)	Carabidae	Trachypachidae	Amphizoidae	Dytiscidae	Hygrobiidae	Noteridae	Gyrinidae	Haliplidae	
1. Antennal pubescence.	present	absent	±	+	+	+	+	+	+	+	(+) Scaratini, Pseudomorphini, Gehringiini—Carabidae
2. Prosternal process.	not well-developed	well-developed	±	+	+	+	+	+	+	+	(+) Omophronini, Masoreini—Carabidae
3. Procoxal cavities open & post-coxal bridge.	combination absent	combination present	±	+	+	+	+	+	+	+	(+) Carabini, Hiletini, Nebriini—Carabidae
4. Prosternal-metasternal contact.	no contact	contact	±	+	+	±	+	+	−	−	(+) Masoreini—Carabidae (−) Bidessini, Vatellini—Dytiscidae
5. Metacoxal cavities.	not interrupted	interrupted	±	+	+	+	+	+	+	+	(+) Gehringiini, Rhysodini—Carabidae
6. Metacoxal fusion.	not fused	fused	−	+	+	+	+	+	+	+	
7. Setal patch.	absent	present	−	+	+	±	−	±	−	−	(−) Bidessini, Hydrovatini, Hyphydrini—Dytiscidae (−) Notomicrini, Noterini—Noteridae

Table 1. Continued.

Character no. and description	Character states		Dytiscoidea								Exceptions within a family-level taxon with a majority of one character state
				Hydradephaga							
	Plesiomorphic (−)	Apomorphic (+)	Carabidae	Trachypachidae	Amphizoidae	Dytiscidae	Hygrobiidae	Noteridae	Gyrinidae	Haliplidae	
8. Giardina body.	absent	present	−/?	?	?	±	+	?	+	?	(−) Hyphydrini, Eretini, Cybistrini—Dytiscidae
9. Internal sac.	large with armature	small without armature	±	+	+	+	+	+	+	+	(+) Rhysodini—Carabidae
10. Vaginal dilator muscle.	absent	present	−	+	+	±	+	+	+	+	(−) Bidesini, Hydroporini—Dytiscidae
Total				+9 −0	+9 −0	+10 −4	+9 −1	+8 −1	+8 −2	+6 −2	(+) 12 (−) 12

obscure phyletic relationship. Therefore, it is not surprising that carabids have gained some apotypic states similar to those of Dytiscoidea. The important aspect is that no group of carabids has gained more than two apotypic states of the characters included in Table 1.

Dytiscoidea and Caraboidea have undergone different rates of adaptive radiation as indicated by their diversity. Trachypachidae, Amphizoidae and Hygrobiidae are groups with less than 10 described, extant species. Gyrinidae (*ca.* 700 spp.), Noteridae (*ca.* 150 spp.), Haliplidae (*ca.* 200 spp.) and Dytiscidae (*ca.* 4,000 spp.) (Britton, 1970) are much more diverse but are still quite a bit less than Carabidae with about 40,000 species (Thiele, 1977). Species diversity is derived by periodic radiation of species known as taxon pulses (Erwin, 1979). Caraboidea have undergone taxon pulses as recently as the Quaternary (Erwin, 1979). In Dytiscoidea, while we lack overall resolution of similar scale, there is no evidence to suggest the action of recent taxon pulses except among a few, widely separated tribes and genera. Presumably extensive, older radiations have taken place such that, with subsequent extinctions, Dytiscoidea is presently comprised of evolutionarily disjunct sets of taxa. This can also obscure phyletic relationship.

At this point we need to examine the classification of Adephaga. Generally, land-dwelling Adaphaga were placed in Caraboidea and aquatic Adephaga were assigned to Dytiscoidea. Therefore, until recently, higher taxa were based on features concerned with way of life. Groups were assigned to families on the basis of similarity of phenotype and assignment of family rank was based on 'appropriate' amounts of dissimilarity (see Ball, 1979 for a general history of classification of caraboids). This same pattern runs throughout the classification of Dytiscoidea. This system may have led to formation of polyphyletic groups. The first major attempt to demonstrate the naturalness of Hydradephaga (as Dytiscidae and excluding Gyrinidae and Haliplidae) is that of Sharp (1882) and his conclusions were that:

". . . although several pecularities may be pointed out as being especially characteristic of the Dytiscidae, yet all of them when taken *seriatim* disappear within the bounds of the family or are found in one or more members of the Carabidae." (Sharp, 1882, p. 967).

Probably the single greatest difficulty in any attempt to establish monophyly is to separate characters which have evolved in parallel as a result of adaptation to aquatic habitats (Bell, 1966)—phenetic similarity—from those which show evolutionary relationship. There are at least two methods by which this distinction can be made. First, is the demonstration of a few, well-founded and well-understood synapomorphies not related to aquatic existence. This would seem to be the preferred method (Hecht and Edwards, 1976). However, this is not yet possible because we lack knowledge of the functional importance of characters in relation to aquatic habitats. A

second tactic is to tabulate a number of characters which, in total, are highly suggestive of monophyly. The supposition of this approach is that the chances of 10 different characters attaining the exact same state in different groups are very low.

It must be understood that the 10 characters in Table 1 are not of equal value. For instance, fusion of the metacoxae (character 6) is probably the best character. Other characters are of lesser value for different reasons, for example, the distribution of the Giardina bodies (character 8) among Coleoptera is too poorly known. Also, characters 1 to 5 are related to an aquatic mode of life (see Discussion of Characters). One way to establish their use as synapomorphies is to examine the character states found in other groups of aquatic beetles outside the Hydradephaga. This analogy will establish whether or not the character states of Dytiscoidea are common aquatic adaptations of beetles, or, whether they may be used as phylogenetic indicators.

The group of beetles best suited for comparison with dytiscoids are aquatic members of the superfamily Hydrophiloidea because of their occurrence in similar habitats to, and their general behavioral similarity to Hydradephaga. Members of the superfamily Dryopoidea and the suborder Myxophaga can also be used, but only to a limited extent because the adaptive zone of these groups is quite different (mainly bottom dwellers with plastron respiration). For Character 1, the majority of adults of all three groups have at least some antennomeres with close set pubescence (Britton, 1970; Reichardt, 1973). As well, a few carabids such as *Carabus clathratus* L. have attained an aquatic lifestyle (Thiele, 1977) yet the antennomeres are pubescent. Therefore, a complete lack of antennal pubescence is not necessarily correlated with aquatic life. Different strategies are employed by these three analogous groups (Hydrophiloidea, Dryopoidea, and Myxophaga) with respect to each of characters 2 to 5. While each of these character states shown by dytiscoids is an aquatic adaptation, they are not the only character states which could be derived in conjunction with aquatic life. Each group has responded to the same situation in a different manner. Therefore, I think they can be used as a basis for inferring monophyly, providing that they are found to be achieved in the identical manner.

Analysis of Table 1 reveals that trachypachids are more similar to Hydradephaga, in the apomorphic states of the characters used, than they are to Carabidae, where they have been placed traditionally. Trachypachids possess nine of a possible 10 derived states and the tenth has not been investigated within the group. They show a striking affinity to a group of families including Amphizoidae, Dytiscidae, Noteridae and Hygrobiidae (Fig. 1). Therefore, the original question is only partly answered—Trachypachidae and at least part of Hydradephaga form a natural evolutionary
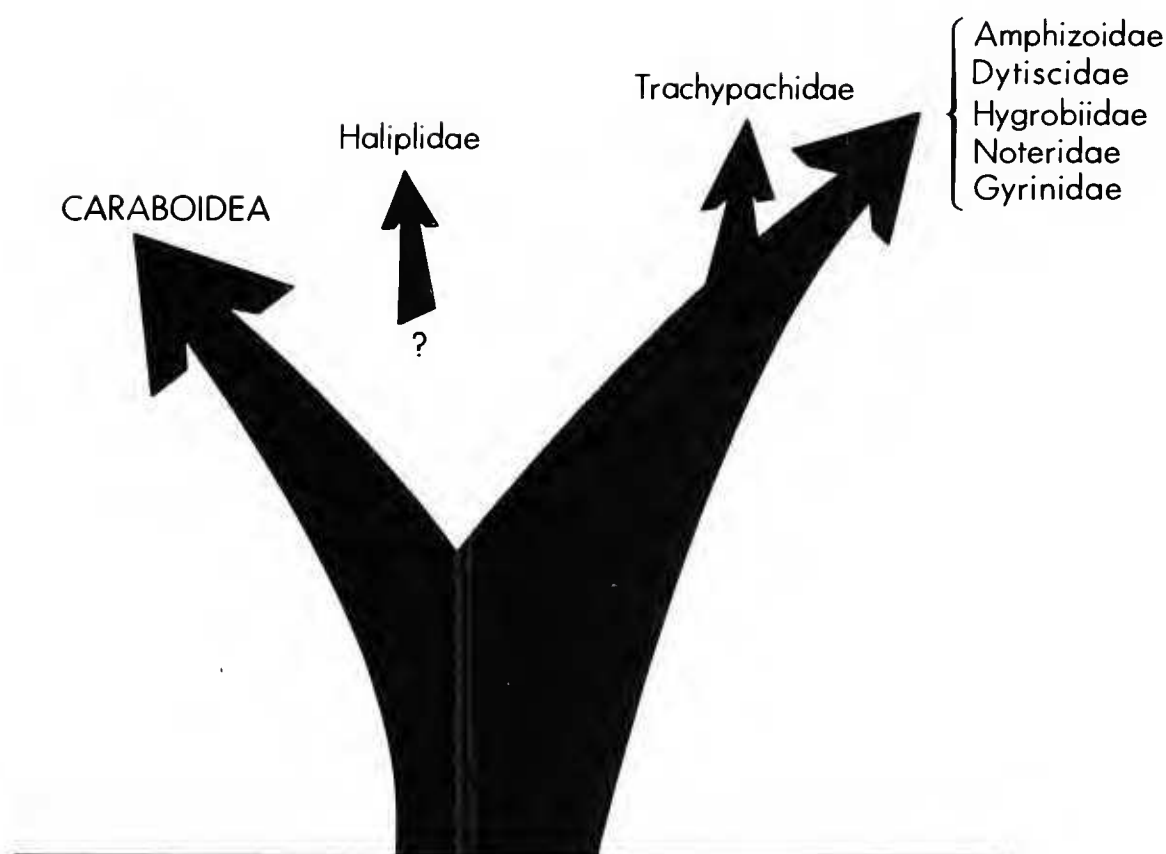
Fig. 1.   Schematic representation of the proposed relationships of Adephaga.

unit. This qualified statement, however, leads to another question—are the Hydradephaga monophyletic?

The characters presented here are insufficient to arrive at a definitive conclusion but they are suggestive of areas where intensive investigation will be helpful. For instance, eight of 12 supposedly independent character losses within family-level taxa of Dytiscoidea occur in a single subfamily (Hydroporinae) of Dytiscidae. Some of these exceptions are probably explained by the small physical size of these beetles (less than 6 mm, Sharp, 1882), but members of Notomicrini and particularly members of *Notomicrus* (1.0 to 1.6 mm, Young, 1978) are among the smallest of Dytiscoidea and yet they are not nearly (one of 12) as autapomorphic. Thus Hydroporinae may not belong with the remainder of dytiscids. If the present classification is to be retained, they must be demonstrated to be closer to other subfamilies of Dytiscidae than to any other group of Dytiscoidea. It is important to note that Burmeister (1976) could find no synapomorphies between female Hydroporinae and the remainder of Dytiscidae, in his study of ovipositor musculature. In addition, Burmeister (1976) could not define a systematic position for *Notomicrus* even though he was convinced that it was not a member of Noteridae.

Haliplidae have only six of 10 synapomorphies with other Dytiscoidea (Table 1) and all but two (Character 1, 2, 3 and 6) are possibly associated

with adaptation to aquatic life. Further, Evans (1977) demonstrated that the metacoxal plates (Character 6) were derived in a manner quite unlike that of other members of Dytiscoidea (see also Sharp, 1882, p. 972). Adults of *Omophron* (Omophronini: Carabidae) have a resemblance in the type of peg and socket mesocoxal articulation (Evans, 1977). However, Burmeister (1976) indicated three synapomorphies between female haliplids, gyrinids and *Noterus* and another six between haliplids and *Noterus*. The position of Gyrinidae must be similarly re-analyzed. The relationships of Dytiscoidea inferred from the characters used in this analysis are shown in Fig. 1.

It should be clear from these few examples that we need more characters, as well as a greater understanding of their functional significance before we can test our existing schemes of classification within Dytiscoidea. This search should be carried out at all levels within the hierarchies of Adephaga. After all, the positioning and rearrangement of higher taxa is only an extension of a systematist's desire to classify species. From an optimistic viewpoint, the beetles have the characters and now all we have to do is go and find them.

One critical question concerning trachypachids remains to be answered. If they are indeed related to Hydradephaga then why do the extant members live in xeric terrestrial habitats (Evans, 1977)? My evolutionary hypothesis is similar to that of Evans (1977), and would have primitive trachypachids in aquatic situations analogous to those in which *Carabus clathratus* occurs (see Thiele, 1977). Subsequent taxon pulses of trachypachids could have given rise to some terrestrial members. As Hydradephaga arose and diversified they replaced the aquatic or semi-aquatic trachypachids, and the terrestrial Trachypachidae are all that remain.

Acknowledgments

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Footnote

[1] Part 1 of A Phylogenetic Classification of Dytiscoidea (Coleoptera).